RETROSPECTIVE

Carl R. Woese (1928–2012)

A visionary microbiologist focused on evolution and discovered a third domain of life, archaea.

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Carl Woese was not a well-known personality outside of microbiology and evolutionary biology, but he forever changed our understanding of the biosphere and its evolution. He passed away at his home in Urbana, Illinois, on 30 December 2012. Carl Woese developed the modern gene sequence–based understanding of biological organization, showing that the evolutionary history of lineages can be tracked to a common ancestral state. In doing so, he discovered the third domain of life, which came to be known as the archaea. His story is the epitome of the outsider, a lone and dedicated visionary who overthrew a century of dogma and established thought and brought about a revolution that has touched every area of modern biology.

An unrepentant iconoclast, Woese skirted popular areas of molecular biology and chose instead to pursue evolutionary questions. He became the foremost expert on all aspects of the genetic code, which he foresaw held the key to a deep understanding of life. His 1967 book *The Genetic Code* broached the notion of a prebiotic "RNA world," still a focus of thought on the origin of life. He made fundamental contributions to how we determine and understand large RNA structures. But Woese's most groundbreaking achievement was his use of primitive nucleic acid sequencing technology to compare ribosomal RNA (rRNA) sequences from diverse organisms, mostly microbes, and to report in 1977, with George Fox, the first scientifically based phylogenetic tree of life—in essence a map that revealed the large-scale organization of life and the early course of evolution.

Woese's findings and interpretations of data clashed with the prevailing scientific wisdom of the time. The model of deep evolution then—still taught in most of our textbooks today—was that all life is one of two kinds, prokaryote or eukaryote, and that prokaryotes gave rise to more modern eukaryotes. Instead, Woese's data showed three kinds of organisms and thus, three domains: eukaryotes, the classic bacteria, and the newly discovered archaea. The concept of prokaryotes had no phylogenetic justification; the eukaryotic nuclear lineage (in contrast to the bacterially derived mitochondria and chloroplasts) did not originate more recently than bacteria or archaea, but was primordial and a sister group to the archaea. These radical claims inflamed many evolutionists, but his three-domain classification is now widely accepted and is supported by much correlation. Woese was personally stung by the harsh criticism, but as he once exclaimed, "I point at the moon and they focus on my finger!"

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One development that Woese did not anticipate was his profound impact on microbial ecology. Microbial ecosystems are the foundation of Earth's biosphere. Yet, before Woese's sequence-based phylogenetic framework developed, there was no meaningful way to survey the microbes that make up the natural microbial world. With Woese's phylogenetic reference framework based on sequences, microbiologists could isolate rRNA and rRNA genes from the environment for sequence analysis, and thus identify and study environmental organisms. Microbial ecology was boosted from a moribund state to one of the most vibrant fields of biology, with important ramifications for medicine, as evidenced by the ongoing Human Microbiome Project.

Woese's discoveries showed that all life on Earth descended from an ancestral state that existed 3.5 to 3.8 billion years ago, with the key elements of the modern cell already in place. Woese regarded the rapidity of this initial phase of life to be the most remarkable aspect of his discoveries, implying that before this time, the nature of the evolutionary process must have had a different tempo and mode from that of the present epoch.

Carl Woese was born in 1928 in Syracuse, New York. He studied mathematics and physics as an undergraduate at Amherst College in Massachusetts, and earned a Ph.D. in biophysics at Yale University in 1953. Being interested in phylogeny, he took considerable pride in his own heritage in physics. His Ph.D. mentor, the biophysicist Ernest Pollard, was a student with physics Nobel laureate James Chadwick, himself a student of the chemist, physicist, and Nobel laureate Ernest Rutherford, who was in turn a student of the physics Nobel laureate J. J. Thomson. Woese developed interests in the origin of the genetic code and ribosome while working as a biophysicist with General Electric Research Laboratory. In 1964, Sol Spiegelman invited him to join the faculty of the University of Illinois, where he remained until his death. He received much recognition over the years, including a MacArthur Fellowship; membership in the U.S. National Academy of Sciences and the Royal Society; the U.S. National Medal of Science; the Royal Netherlands Academy of Arts and Sciences Leeuwenhoek Medal, considered the highest award in microbiology; and the Royal Swedish Academy of Sciences Crafoord Prize in Biosciences, a parallel to the Nobel Prize.

Although he pursued his life's work with a dedication, intensity, and even gravitas that has rarely been matched, Woese imbued his research with a personal sense of fun and playfulness. He was a complex man, but those with whom he was able to share his passions found him brilliant, witty, brutally honest, generous, and humble. Woese often attributed his success in biology to his training as a physicist. Once, appalled by an immodest parody of a famous quote by Newton, he quipped: "If I have seen further than others, it is because I was looking in the right direction." Woese indeed saw miles ahead of the rest of us. His passing leaves the microbiology community feeling, as he would surely put it (and with a nod to his love of jazz), "kind of blue."

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